stated in a letter from Mr. W. F. Kirby, to whom specimens were submitted; but that is a larger species with a considerably longer oviscapt in the female. The location of this species in the genus *Aplopus* is merely tentative, the brachypterous males excluding it from this genus unless the male of *micropterus*, the type, is proved to be also brachypterous. In that case the species with macropterous males would necessarily take another generic name.

Class III, ARACHNIDA.

Order II, ARANEIDA.

CHANGE OF COLOR AND PROTECTIVE COLORATION IN A FLOWER-SPIDER. (MISUMENA VATIA THORELL).

BY ALPHEUS S. PACKARD, LL.D.,

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My attention was called to this interesting subject in the summer of 1903, by observing the adaptation or "mimicry" of our common *Misumena vatia* Thorell (*Thomisus fartus* Hentz) to the hues of the petals of the daisy fleabane (*Erigeron annuus*) in blossom at Merepoint, Brunswick, Maine, July 18. It was then my impression that this spider was known to change its color, and I suppose that this took place within a short period — a few days at least — but on trying to find mention of such rapid or any other change of color I was unable to meet with any such notices. As for my own experience previous to last year I have only a vague recollection of seeing many years ago on a tree or flower a yellow *Misumena*. On inquiry of Mr. Nathan Banks, he very kindly called my attention to a brief note by James Angus in the American Naturalist, Vol. XVI, p. 1010, which says: "I suppose you know the little flower spiders, that conceal themselves in the flowers, and seize any unwary insect that may chance to come within their reach. I have generally found them white and yellow. I suspected they changed their color, and by experiment I find that this is so. If I take a white one and put it on a sunflower, it will get quite yellow in from two to three days. I believe they capture almost anything, but they seemed to be partial to the bees. I

found one the other day with a wasp; the latter was not yet dead, but it was tightly held by the throat by the spider. The next day the wasp was found lying dead under the flower." Mr. Banks also wrote me October 7, 1903, as follows:

"I do not remember that there has ever been published any positive evidence that *Misumena vatia* or the closely allied *Runcinia aleatoria* ever change their colors. Of both species yellow and white specimens are found sometimes marked with red. I think Miss Treat once published a note to the effect that *Misumena* when placed on a different flower returned to its former flower. There is a case on record (Nature, 13 April, 1893, p. 558) where a Mr. Bell states that an African bluish spider when captured turned brownish, and afterwards gradually recovered its bluish color, perhaps from fright!

"Personally, I believe *Misumena* changes color, at least from white to yellow. From old notes I take the following: Early in the spring where the principal large flowers are white *Trillium* (wake-robin) I have found many white *Misumena* with a red stripe; later, when the *Trilliums* were faded, there were many *Misumena* on the yellow dog-tooth violet; these were all yellow, with red stripe. On this area were no white flowers then, and no *Misumenas* to be seen except on the *Erythroniums*.

"This, of course, is no proof, but evidence. I don't see anything strange or rather new if they did change color. For the young *Misumena* is neither white nor yellow, and without red stripes. Yet from these almost hyaline young grow spiders, some white, some yellow, some with red stripes. Therefore it would seem that their color depends upon their surroundings. If these surroundings can develop a yellow from hyaline, why not yellow from white?

"I have seen *Misumenas* on flowers and plants with which their colors did not harmonize; and there is variation in the shade of yellow and in size of red stripes and, with *Runcinia*, in the number of these stripes."

On the 18th of July, 1903, I detected a medium sized *Misumena vatia* holding in its jaws a green fly (*Lucilia cæsar*). It had fastened its jaws in between the head and thorax, and there remained motionless several minutes until I touched the tip of the fly's wing, the fly being dead, and disturbed the spider so that it let the fly drop to the ground.

The flower of this fleabane is like an aster, *i. e.*, with a bright yellow center and pale, whitish lilac petals. The abdomen of this spider was yellowish and the head, thorax and legs pale whitish, but not snow-white, and more livid than the petals of the flower when the spider was resting directly on top, but when the legs were held obliquely so that the light was oblique, the hue or effect was exactly like that of the petals, so that it was a decided case of cryptic or protective mimicry.

A couple of days after I found several more half grown spiders on the same kind of flower, one had seized a small fly by the neck. One was found on the ox-eye daisy or white weed; it sat on one side of

the yellow center, on the white petals; the fly alights on the flower, probes the yellow flowerets head-down, when it is seized by the neck and its blood is sucked; this spider and two others on the fleabane were all whitish, both cephalothorax and abdomen, the latter whiter than the cephalothorax and legs. No yellow ones were seen this season, but it did not occur to me to look for them on the golden rod.

I tried several experiments to see if these spiders would change colors. I enclosed one small one in a test tube on the red corolla of *Rudbeckia* for an hour, without any perceptible change, and again put six in the tube for a day without any change. Four of the *Misumena* were kept for four or five days in a bottle filled with wild rose leaves but no change was observed. They were fed with house flies and never appeared to see or notice the flies until the victim actually flew or ran directly into the jaws of the spider. Also in neither season did I find any reddish spiders on the wild rose.

The remaining observations were made at Merepoint, in July, August and September of 1904. On the 8th July of I found two on the buttercup; neither were yellow, but of the usual pale slightly greenish tint; a small one detected on the 12th was of a slight yellowish green. July 12 two decidedly white ones occurred on the buttercup, one with a red stripe on each side of the white abdomen. I placed two of them in a bottle filled with buttercup flowers, and kept them for three or four days without noticing any change of color. Four examples were collected from the ox-eye daisy, but none were yellow, one was whitish and the other greenish. One large one was yellowish green.

July 14 I put one in a box filled with heads of the ox-eye daisy, it was faint yellowish, while one in a test-tube with the same kind of flower is yellowish green. A rather large *M. vatia* was found with an *Andrena* bee 12 mm. long in its jaws.

I lined a glass bottle with tiger lily leaves and left a large white one with red lateral stripes in it for three or four days, but no change resulted.

After this, with the flowering of the golden rod, the prevalent color became yellow. The golden rods began to flower July 31, and on that day five small whitish ones with no yellow tinge were found on the freshly opened flowers. Four days after (August 4), when more *Solidago* flowers had opened six small spiders were picked off, and one half-grown spider all yellow, distinctly so, the cephalothorax and

abdomen above and beneath, and also the legs. This is the first yellow one I have seen for some years. The yellow hue is uniform, though the abdomen was a little deeper in hue than the rest of the body.

Two days later (August 6) the yellow ones had greatly increased in number with the blossoming of additional plants of the *Solidago*, for now ten yellow ones were found to one on the 4th.

The spiders were thoroughly well protected from observation, both by their pale yellow color, and by their habit of hiding among the greenish yellow calices of the flowers, not resting as a rule on top of flowers.

Was the change of color due to alteration of the pigment, or to color-preference? Had the yellow ones simply gathered on the newly opened golden rod and come from the yellow flowers? Evidently not, because there were no other abundant yellow flowers, the buttercup having mostly gone out of blossom, and the only other flowers on which they had been detected were the fleabane, ox-eye daisy, and wild rose, these being the commonest flowers at Merepoint.

During the latter part of August yellow ones prevailed on the golden rod. On the 12th I found three rather large yellow *M. vatia* on the golden rod, one large one striped on the side of the cephalothorax and abdomen. Only the young ones were whitish. It seems quite apparent that the yellow ones have more or less gradually changed, since they are not of the exact shade of yellow, the hues differing in intensity as if they had gradually become adapted to the change of color, and they are all yellow with a shade or tinge of green so that they are more in harmony with the general greenish yellow of the heads of the flowers among which they hide; as they are not, at first at least, of a uniform deep straw-yellow it is evidently a case of gradual adaptation, and not simple color preference, which assumes that the spiders were originally yellow and migrated to the *Solidago* from some other plants.

August 15 I found two small white ones on the golden rod and three or four yellow ones, and through the month middle and large-sized yellow ones occurred, with young colorless or whitish ones.

That they do change in consequence of adaptation to the yellow of the golden rod seems quite satisfactorily demonstrated by my beating from the golden rod, eighteen *M. vatia* into the umbrella, all of which were distinctly yellow, besides an additional small whitish one.

Afterwards at Intervale, N. H., on September 8 and 9, I found the yellow ones on *Solidago canadensis*, the most common species, and on *S. rugosa*, less common there, although this is the most common. Quite small yellow ones occurred, and at Providence several large deep uniform yellow ones.

Afterwards, on September 16, at Chocorua, five or six yellow *M. vatia* occurred on the golden rod (*S. rugosa*), one young *M. vatia* was yellow, the other greenish-yellow, all the young being distinctly yellow; one large example of a deep yellow. Not a single white half-grown or fully grown was seen.

September 17 in collecting I had the same experience as on the previous day; I found several young *M. vatia* which were yellowish and two large fully grown deep yellow ones, but no white ones occurred. On the red flowers of *Canna* occurred one full grown *M. vatia* with greenish cephalothorax and legs and a white abdomen. I beat the heads of a patch of life everlasting, comprising over 100 or 200 flowers, without finding a single spider on them, and none occurred in the few white and purple asters examined.

On reaching Providence, after considerable search I found but a single *M. vatia* on the golden rod, on the other hand *M. asperata* was the common species here, during the last week of September. Although the general effect is reddish, the ground color is pale yellowish; though in large ones the ground hue is often reddish. One yellowish one occurred on a small sunflower. It molted September 26. By the 4th or 5th of October, very few were seen, as they had apparently left the plants and gone into winter quarters.

At Chocorua yellow *M. asperata* occurred on the sunflower and also on a yellow gilly flower, or a similar plant.

Occurrence of a white M. vatia on a white golden rod. — At Intervale, N. H., I found two white ♀ *M. vatia* on the pale whitish golden rod (*S. bicolor*), and as stated above I found a white ♀ on the same species of golden rod at Providence. It was marked with red on the sides, as usual.

Occurrence of M. vatia on the sunflower. — At Intervale I found a large deep yellow spider of this species on the wild sunflower, *Helianthus decapetalus*.

Experimental proof of change of color. — On the 9th of August I enclosed two white *M. vatia* in a bag made of mosquito netting and tied over a head of the flowers of the golden rod. On the 15th on

opening the bag I found one which had grown larger, but still remained white, certainly not yellow.

August 20 I again opened the bag; the largest one was greenish white on the cephalothorax and legs, but the abdomen was pale yellowish; the smaller one had become yellowish all over, the body and legs distinctly yellowish, and the abdomen a little deeper yellow. This seemed a good test, and so far as a single experiment indicates, it shows that the change of color does occur in middle life, or when the spider is about half grown. The change evidently takes place in the pigment of the integument, as the result of exposure to yellow light reflected from the yellow flowers. In this way the spiders become adapted to their yellow environment.

The change requires certainly more than two or three days, *i. e.*, about a week or ten days. Thus on the 23d of August I placed a single white *M. vatia* found the day previous on the golden rod, in a bag containing a full head of yellow golden rods, and on opening it three days after (the 26th) it had not changed. On September 3 I opened the same bag and found the cast skin of the same white spider, the spider was not of full size, it was not distinctly yellow, being still whitish, with a greenish abdomen but slightly tinged with yellow. There was a dark green line on each side of the cephalothorax. Unfortunately the bag was not again opened, as I failed to return to Merepoint and was thus prevented from afterwards examining the specimen.

PREVIOUSLY PUBLISHED NOTES ON CHANGE OF COLOR IN FLOWER SPIDERS.

The foregoing observations were made and written out either before meeting with the published observations of others, or if read in former years they had been forgotten.

Besides the note published by Mr. Angus, Mrs. Mary Treat * states that *Thomisus celer* which lives in the heart of roses is nearly of the same shade of color as the red flower, and that when the spider is "waiting for prey she cuddles down in the center of the flower and erects her legs, when it is almost impossible to distinguish them from the imperfect scattering stamens." Mrs. Treat also observed a spider catch a butterfly, and adds that she had often noticed the remains of of night-flying moths scattered near her, which she had evidently captured during the night.

* My garden pets, Boston, 1887, p. 12.

That butterflies may occasionally be seized and destroyed by these voracious spiders is farther proved by Mr. Firmen* quoted by Mrs. Peckham. He once saw two butterflies "in the clutches of a spider," and on another occasion "witnessed the actual capture of a small blue butterfly (*Lycænestes*) by a white spider of the same genus" (*Thomisus*).

Returning to the subject of a change to rose-red, which I have not myself observed, Firmen mentions seeing at Cape Town a species "of the exact rose-red of the flowers of the oleander; and to more effectually conceal it, the palpi, tops of cephalothorax, and four lateral stripes on the abdomen, are white, according remarkably with the irregular white marking so frequent on the petals of *Nerium*."

Rev. O. P. Cambridge† has found *Thomisus onustus* pink when upon heather blossoms, and quotes Rev. C. W. Penny to the effect that it is yellow when upon yellow blossoms.

Prof. Edouard Heckel‡ has described and illustrated with two colored plates the color variations of *Thomisus onustus* — a species abundant in the south of France. This spider frequents the flowers of *Convolvulus arvensis*, and is so abundant during the months of August and September that nearly every plant has its spider; it is evident, therefore, that, in spite of the numerous insect visitors to these flowers, there must be a certain amount of competition for food among the spiders; this is especially the case if it be true that the spider limits itself almost exclusively to two Diptera, ignoring the other insects. The flowers of this *Convolvulus* show three varieties: one is pure white; another pink, with traces of a vinous red externally; while the third is a paler pink tinged with green externally. These three varieties of the *Convolvulus* are inhabited by three varieties of the *Thomisus* which correspond exactly in their hues with the flower, with the exception of the one which lives in the white flowers; this variety of spider has a blue cross on the abdomen, and the extremities of its legs are likewise bluish. Blue, however, may be suggestive of shadow, and not render the animal very conspicuous. These three varieties do not embrace all the colour modifications of which the spider is susceptible; it becomes a dark red when upon the flowers of *Dahlia versicolor*, which has a similar colour, and yellow when upon the flowers of the yellow *Antirrhinum majus*.

That I failed to find any bluish individuals is probably due to incomplete observations, since bluish individuals may yet occur in New England. That no pink ones occurred in the flowers of the wild rose examined may be due to the fact that those found by me may not have

* Protective resemblances and "Mimicry" in animals, p. 4.

† Spiders of Dorset.

‡ Bulletin Sc. France et Belgique, XXIII, 1891. Quoted from Beddard's Animal Coloration, p. 111.

been long enough exposed to the reflections of the roseate petals of this flower.

Beddard (Animal Coloration, p. 113) suggests that the yellow color of the *Thomisus onustus* is "not adaptation but simply due to age." It once occurred to me that this might be the case, but I think that the facts I have stated are more strongly in favor of a slow adaptive change, and it is disproved by the fact that old, fully grown white examples frequently occur throughout the last of the summer season.

Mr. Cook,* referring to what was probably *Misumena vatia*, quotes from an article by L. C. Palmer, "an intelligent observer, but not a naturalist," to the effect that he found a species of spider near Philadelphia which was purple on the purple boneset, pure white on the white panicle of the boneset proper, while on the golden rods it was yellow.

In Italy Pavesi "finds that this same species when living on flowers is white, or white and yellow with red stripes on the abdomen; but that when found among the grass it is grass-green, with dark, obscure stripes on the cephalothorax and palpi." (Quoted by Mrs. Peckham, l. c., p. 88.)

Mr. Emerton † found *M. asperata* perched on a flower of sorrel (*Rumex acetosella*), its colors being exactly those of the flowers. In "The Common Spiders of the United States" (1902) he states that the *Misumenas* live on plants, among the flowers, especially on large flat clusters like those of carrot and thoroughwort. "Whether," he says, "spiders prefer flowers colored like themselves is an unsettled question; at any rate *Misumenas* of all colors and both sexes have been found in white flowers. Occasionally individuals are found on flowers of exactly the same color as themselves; for example, deep yellow *M. aleatoria* on the wild indigo *Baptisia tinctoria*, and the reddish *M. asperata* on the flowers of sorrel."

The probable cause of the change of color. — The change of color in the flower spiders appears to be due primarily to the direct action of the sun's light, and secondarily to the absorption of the color light-rays by the pigment of the integument. That it is obviously in no way the result of the food is evident, because these spiders feed upon the colorless blood of insects. We know nothing of the immediate cause of such changes, which occur during the life-time of the indi-

* American spiders and their spinning work, II, p. 368, 1890.

† Spiders of the family Thomisidæ, Trans. Conn. Acad., VIII, 1892, p. 370.

vidual, and are not transmitted to the offspring, beyond the fact that they are due to differences in the colorational environment, *i. e.*, the white, or yellow or pink hues of the flowers in which the spider hides or on which it rests.

The explanation of the cause must be sought in what we regard as a parallel case in the experiments initiated by T. W. Wood* in 1867, and greatly extended by Professor Poulton,* as described in his able essay "On the color relations between certain lepidopterous pupæ, and the variously colored surfaces immediately surrounding them." Mr. Wood found as the result of his experment that "the skin of the pupa for a few hours after the caterpillar's skin has been shed is 'photographically sensitive,'" and "as might be expected, by putting the specimens in the sunshine at the time of changing, and surrounding them as much as possible with any desired colour, the most successful results have been obtained."

Professor Meldola has pointed out, says Poulton, that the theory of the moist, fresh, pupal surface as "photographically sensitive" was obviously a metaphor borrowed from the sensitive plate of photography and that there can be no real analogy between the two processes. Poulton concludes that the problem is essentially a physiological one, and that the physico-chemical changes are "merely the results of far more complicated physiological processes."

The question arises whether the change in *M. vatia* is connected with the molting period, but I have no observations which directly prove this. It is well known that many spiders with nearly each molt appear in different colors, or undergo some change in the markings.

Summary of Results of My Own Observations.

1. In the early part of the summer (June and July) when the greater mass of flowers are the white fleabane and the ox-eye (the wild rose and buttercups excepted) the spiders (*M. vatia*) are white and no yellow ones were detected.

2. Later in the season, towards the end of July (July 30–31), and early in August when the golden rod in Maine begins to flower, a few of the spiders are yellow, but by the middle of the month and through September they are almost without exception yellow, varying from a pale to a deep hue, probably due to the length of time they have been

* Trans. Ent. Soc. London, 1867, p. XCIX–CI.

† Philosophical Trans. Royal Soc. London, vol. 178, 1887, p. 311.

on or among the yellow flowers; an occasional white one occurring which may have been a recent arrival from some bush or other plant.

This is an exact parallel with the instance observed by Mr. Banks, when the spiders occurring early in the spring in Virginia on the white trillium, afterwards become yellow on the yellow flowers of the dog-tooth violet, there being no white flowers in the neighborhood.

3. By enclosing a couple in a bag tied over a golden rod they have actually been found to change from white to yellow in the course of ten or eleven days.

4. There is an actual change in color, and the assembling of yellow spiders on yellow flowers is not a case of color-preference, but of a gradual alteration in the color of the pigment of the integument. Whether as in the case of lepidoptera, the change takes place at or directly after the time of molting has yet to be ascertained. I have no observations directly bearing on this question.

5. In rare cases (3) white *M. vatia* were collected on the white *Solidago bicolor.*

6. No *M. vatia* or any other species of Thomisidæ were found on blue or white asters or on life everlasting, of which hundreds were examined.

7. The result of the coloring, while in harmony with the color environment, is certainly not to protect the spider from the attacks of birds, as the only kind of spider-eating bird is the humming bird, other kinds of birds, as investigation shows, not feeding on spiders. On the other hand, the coloration is so far cryptic that flies and other prey of the spider less easily observe its presence. This, however, is quite a subsidiary matter; without reference, so to speak, to the biological environment, the main fact is that the color of the spider is the mechanical result of exposure to an environment of this or that color.

8. The cause of the change of color is simply the action of light, and in the case, for example, of yellow individuals, to the reflection of yellow light from yellow flowers continued for a period of exposure varying from several days (three or four) to one or more weeks. There are multitudes of similar cases in other groups of animals, and protective coloration so-called is simply the mechanical result of the operation of a primary physical agent, *i. e.*, light.

The colorational change is not due to natural selection or to the survival of some one or even several fittest individuals, since hundreds

of thousands or great multitudes of individual spiders living on the golden rods of a vast area extending over northeastern America appear to become similarly affected when the golden rods come into flower.

In this case the color is not necessarily hereditary, since the young spiders are at first colorless, and when older whitish. The yellow hue persists only as long as the flowers are in blossom. Thus the yellow color variety persists only as long as the colorational environment is the same. Hence the natural selection theory seems quite inadequate and also unnecessary to account for the apparent mimicry, and the change of color is a clear case of adaptation to a color-environment, and is an example of Lamarckism, or what Eimer and others call orthogenesis.

Since this paper was sent for publication, we have read Keeble and Gamble's elaborate memoir on the color physiology of the higher Crustacea which fully confirms our view that color changes are primarily due to light and environmental changes. The change of color in the flower spiders seems to be an example of what Pouchet calls the "chromatic function." He experimented by placing shrimps (*Palæmon* and *Crangon*) in black and white dishes in broad daylight. On the black background the pigment cells expanded, and the resultant coloration was a dark one in harmony with the tone of the surroundings. On the white background they contrasted, and the consequent colorless place presented no contrast to the adjacent surfaces. Pouchet claims that the pigment movements were due to the stimulus of light, eletricicty and certain drugs, and he concluded that the background or color of the environment determined the movements of the chromatophores or pigment cells, through the mediation of the eye and nervous system.

His results have been confirmed and extended by Keeble and Gamble* in their recent work, from which we have taken the above abstract of Pouchet's results. They also record that Jourdain (1878) pointed out that in addition to light, electrical and pharmacological stimuli, the temperature of the water influenced the color of sensitive crustacea, and that such changes were naturally independent of the action of the retina. Keeble and Gamble have shown (1900) that "rapid movements in the chromatophore could be induced by any decided stimulation; that slow changes followed the application of

* Phil. Trans. Roy. Soc. London, vol. 196, pp. 295–388. 1904.

less powerful stimuli, such, for example, as differently colored backgrounds in place of strongly contrasted ones; and that underlying these quick and slow reactions of the chromatophores to changes of environment, there was at least one intrinsic chromatophoric rhythm, the after effect of alternating night and day."

They confirm the view that light sets up movements of the pigments by its direct action on the chromatophores. "Light exerts a potent and varied influence on the littoral crustacea. Such animals as *Hippolyte*, *Mysis*, and *Palæmon*, instead of becoming inured, remain highly susceptible to the ever-changing light conditions of their environment." It also plays an important part in controlling not only the movements of these animals, but also the distribution of their pigments. The factors in pigment-movements are intensity, background or environment, and monochromatic light.

The color-phases in shrimps depend on different light conditions. In darkness the pigments of *Palæmon*, etc., are so contracted into their chromatophore-centers, that the latter appear as minute dots, resulting in a transparent phase. The rapidity with which the change takes place varies from ten or a less number of minutes to an hour or two.

What the authors call the "white background phase," *i. e.*, a transparent condition, the pigments being freely contracted, may be and generally is assumed with great rapidity, less than a minute often sufficing to call it forth in *Hippolyte* or *Macromysis flexuosa*. Here we might add that Pouchet found that in the turbot under certain conditions the color changes are only developed after a period of several days. Very pertinent to the matter of change of color in spiders and insects are the author's conclusions as to the environmental or background effects on littoral crustacea. "The background effects on pigment-movements, help us," they say, "to imagine how light modifies pigment-development and thus causes such an animal as *Hippolyte* to 'give into' its surroundings, modelling its diurnal pigment distribution on the distribution of light and shade on its background." They add: "As long as its background is unchanged, change of intensity avails little. Now of all things which characterize *Hippolyte* its tenacious immobility on the weed of its choice is the most striking."